RIGHT-HANDED AND LEFT-HANDED CORN EMBRYOS

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The vertical stem of a corn plant, with its two rows of leaves arranged in a plane, has the appearance of a bilaterally symmetrical structure, but a close examination shows that this appearance is deceptive. The sheath of each leaf of such a plant is wrapped around the internode with its edges overlapping. If the observer imagines himself as standing in the position of the internode of the stem, with the leaf sheath around him like a coat, he will find that sometimes the right half of the sheath overlaps the left, and sometimes the left overlaps the right. For convenience we shall designate the one as dextral, or right-handed, and the other as sinistral, or left-handed. Further examination of the plant reveals that the dextral and sinistral leaves are arranged in alternate sequence along the stem. Thus it follows that the overlapped sides of the sheaths all fall on one side, and, if we should split the plant lengthwise in the plane of the midribs of its leaves, one half would have only the overlapping sides of the sheaths and the other would have only the overlapped sides (pl. 34).

This asymmetry of the shoot, which is characteristic of almost all grasses, is further shown in various species by other characteristics. Usually there is some difference between the two sides of the collar at the top of the sheath; the auricles, when present, ordinarily show some differences and alternately reverse their direction of overlapping in successive leaves; the leaf blade is frequently asymmetrical; and the insertion of the base of the sheath marks a spiral line on the stem. This structural pattern may be regarded as a sort of morphological dorsiventrality, but it is apparently not always correlated with orientation in rhizomes, stolons, or other horizontal stems.

Since the overlapping edge of the sheath is inserted on the stem a little lower than the overlapped side, it follows that the line of insertion of a right-handed leaf describes a left-handed spiral, and that of a left-handed leaf a right-handed spiral. This reversal of direction of the spiral at each node is an aspect of the phenomenon known as *antidromy*, which received much attention, especially from German morphologists, during the latter half of the nineteenth century. It occurs in one way or another in many kinds of plants and has been cited in objection to the theory that the distichous arrangement of the leaves of a grass can be interpreted as a form of spiral phyllotaxy (Elias, 1942, p. 29).

The significance of this reversal of pattern in consecutive phytomers has never been fully explained. As far as the grasses are concerned, it is only a part of a more comprehensive pattern in which various other structural differences appear in successive internodes. In some species, for example, the stem has alternately long and short internodes, the short ones sometimes being so reduced that the leaves appear to be opposite (pl. 34).

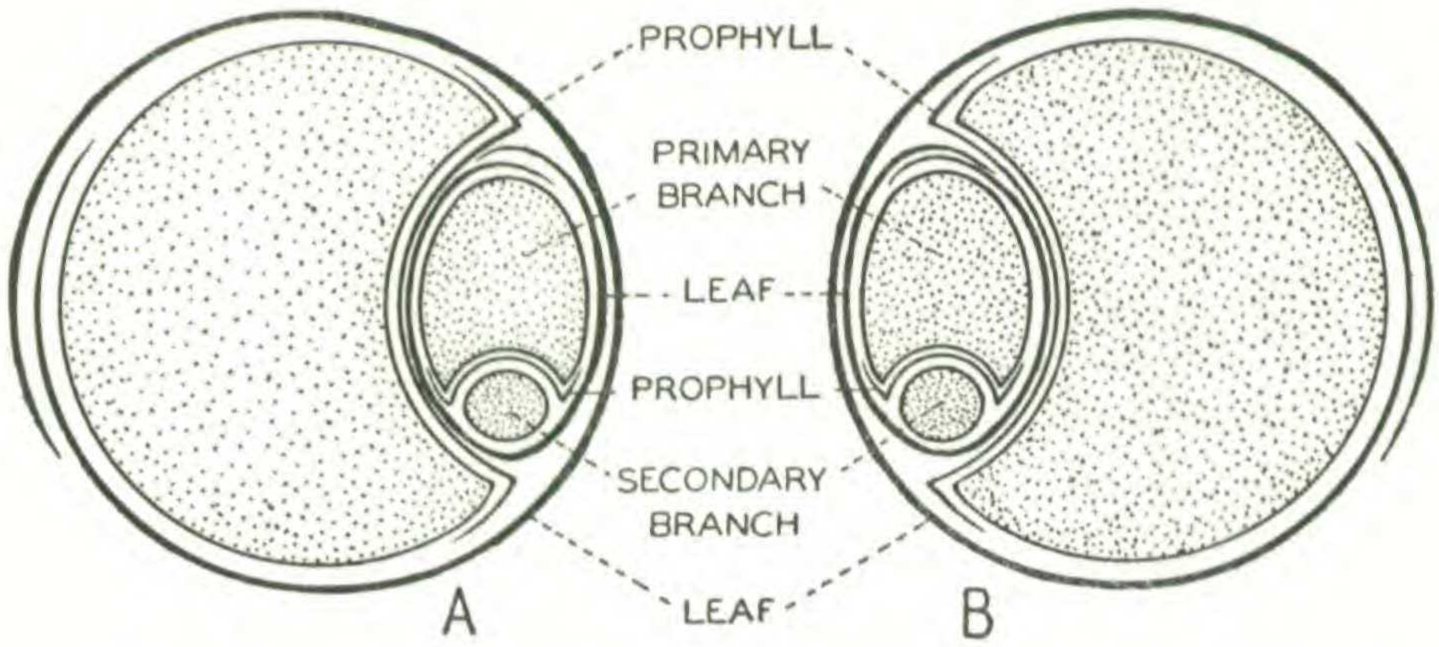

Fig. 1. Cross-sections of two consecutive internodes of a corn stem, showing leaves and axillary structures. A birdseye view of the structural pattern of the plant can be produced by superimposing one of these diagrams on the other. Note that the overlapping edges of the leaf sheaths are both on the same side of the stem and that the secondary branches both fall on the opposite side.

It is obvious that every individual grass seedling must start out in life as either a right-handed or a left-handed plant, as being determined by the direction of the overlap of the sheath of its first foliage leaf, the coleoptile being excluded from consideration. When a large number of embryos of any one species are classified as dextral or sinistral, the ratio is approximately 50:50. This can readily be demonstrated by examining the seedlings grown from a handful of corn.

When a branch arises in the axil of a leaf, its true foliage leaves (the prophyll excluded) fall in a plane which cuts at right angles the plane of the leaves of the main stem (fig. 1). The sheath of the lowest leaf of the axillary branch ordinarily overlaps in the same direction as that shown by the leaf subtending the branch; that is, right-handed branches arise in the axils of right-handed leaves and left-handed branches in the axils of left-handed leaves. To this there are, however, occasional exceptions.

Furthermore, the first leaf of a branch, with whatever axillary structure it may subtend, is located on the side of the branch next to the overlapped side of the subtending leaf of the main axis. From this there may result a peculiar picture in a grass which branches profusely. Suppose we have a vertical grass stem whose leaves stand in an east-west plane, with the overlapped edges of its leaf sheaths all on the south side. In the axil of each leaf there develops a branch, the plane of whose leaves extends north-and-south. Each of these primary branches produces a branch of the next order in the axil of its lowest leaf. All these secondary branches will then fall on the south side of the plant, producing at first a very asymmetrical structure.

This same pattern of asymmetry is carried into the inflorescences of many grasses as far as the branching of the various axes is concerned. Ordinarily nothing comparable with the regularity of the overlapping of leaf sheaths can be detected, for the simple reason that grass inflorescences seldom have bracts sufficiently

developed to overlap. It is generally conceded that at least the glumes and lemmas of the spikelet are reduced leaf sheaths, but they are usually not broad enough to encircle the rachilla and overlap.

Toward the close of the past century a number of interesting cases of antidromy were reported and discussed in a series of papers by George Macloskie (Macloskie, 1895, 1896, 1896a, 1896b). Many of the plants with which he deals are outside the grass family, and I have not examined them, but one observation on the structure of the ear of corn is obviously not plausible, and I have been unable to substantiate it by re-examining the material. The point in question is not one of great consequence, but it does involve an interesting fact. Moveover, Macloskie's statement has been cited in at least one later study (Elias, 1942, p. 29) and will, if not corrected, continue to lead to confusion. A refutation seems, therefore, to be in order.

The problem can best be presented by quoting the following extracts (Macloskie, 1895, pp. 379–380). The italics are mine.

> "It was then shown that . . . . . there must be two kinds of plants of every species of the order [Gramineae]; the one kind or 'caste' has its lowest foliage leaf . . . . . with the right margin of its sheath overlapping the left margin, 'dextrally infolded' as I term it; and the other caste has the left margin overlapping the right, 'sinistrally infolded. . . . . Thus it became manifest that as there are two castes of the maize plant, so there are two castes of grains, the one being the 'antidrom' of the other . . . . . ."
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> "The ear consists of columns each containing a pair of rows of grains; we may designate the row opposite our right hand as dextral and the other row (opposite our left) as sinistral. It was soon made out that in the particular ear examined *the grains of the dextral row were all with dextral embryos, and those of the sinistral row had sinistral embryos.* Whether this law would apply to all the ears on one plant, or whether the order would be inverted between the ears arising from successive nodes, or between the ears of different plants, is yet to be determined. On examining the very young ear of maize I found the grains of the paired rows of each column oriented close to each other, almost face to face, the young styles running up together, and a gap between the adjoining two-rowed columns.
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> "From this discovery the inference was obvious that the seeds of corn differ from each other antidromically, *according to the side of the placenta or axis from which they arise; that their embryos vary in consequence, and determine the caste of the future plant.*"

From the above it is obvious, in the first place, that Macloskie was confused in his understanding of the morphology of the ear of corn. A pair of rows of grains is not at all the morphological equivalent of two rows of seeds attached to a linear placenta. Furthermore, on theoretical grounds, I have for many years questioned the accuracy of his observation. Granting that the general antidromic pattern of vegetative structure of a grass plant is as described, there still seemed to be no plausible reason why it should affect the pattern of the embryo. The characteristic pair of grains of corn is borne in two separate spikelets on a short branch arising from the side of the cob. These two spikelets, representing secondary branches on this short primary branch, might be expected to reflect the normal antidromic vegetative pattern even though this be difficult to detect. But why should the pattern continue into the embryos, which are entirely separate morphological entities?

Macloskie seems to have had some misgivings about his thesis and leaves the way open for amendment in the light of further study. As far as I have been able to learn, no later report was ever made. He does not indicate how many pairs of grains he examined, but the number must have been small. Over a period of some five or six years we have from time to time examined individual ears of a dozen or more varieties from widely separated localities, and in not one of them have we found verification of Macloskie's statement. In practically every instance, the examination of only two or three pairs of grains was sufficient to refute it.

In the early studies, the ear selected was held with its tip up, and grains from the left and right rows of a pair were removed and planted separately. The following classification of embryos represents a combination of the results secured from several pairs of rows of a commercial dent variety. It is typical of the results from several ears studied in this way.

Sinistral embryos in grains from left row	114
Dextral embryos in grains from right row	128
Dextral embryos in grains from left row	121
Sinistral embryos in grains from right row	111

It will be noted that only those embryos of the first and second categories, approximately 50 per cent of the total number, conform with Macloskie's statement. The other two classes should not have occurred at all.

But the error as to the structural pattern of the individual *pair of spikelets* is really greater than indicated above. This is disclosed by a comparison of the right and left grains of individual pairs. Paired grains were planted side by side, and the paired seedlings fell into the following classification:

Pairs with left embryo sinistral and right dextral	95
Pairs with both embryos dextral	130
Pairs with both embryos sinistral	95
Pairs with left embryo dextral and right sinistral	104

Of these four classes, only the first, approximately 25 per cent of the total number, conform with Macloskie's statement. The second and third classes may be said to be half right as far as individual grains are concerned, but wrong as an expression of the pattern of the pair. The third class is entirely wrong.

From these observations it is evident that the type of embryo—sinistral or dextral—is determined solely by chance. It is in no way correlated with the position of the grain in the typical pair of spikelets.

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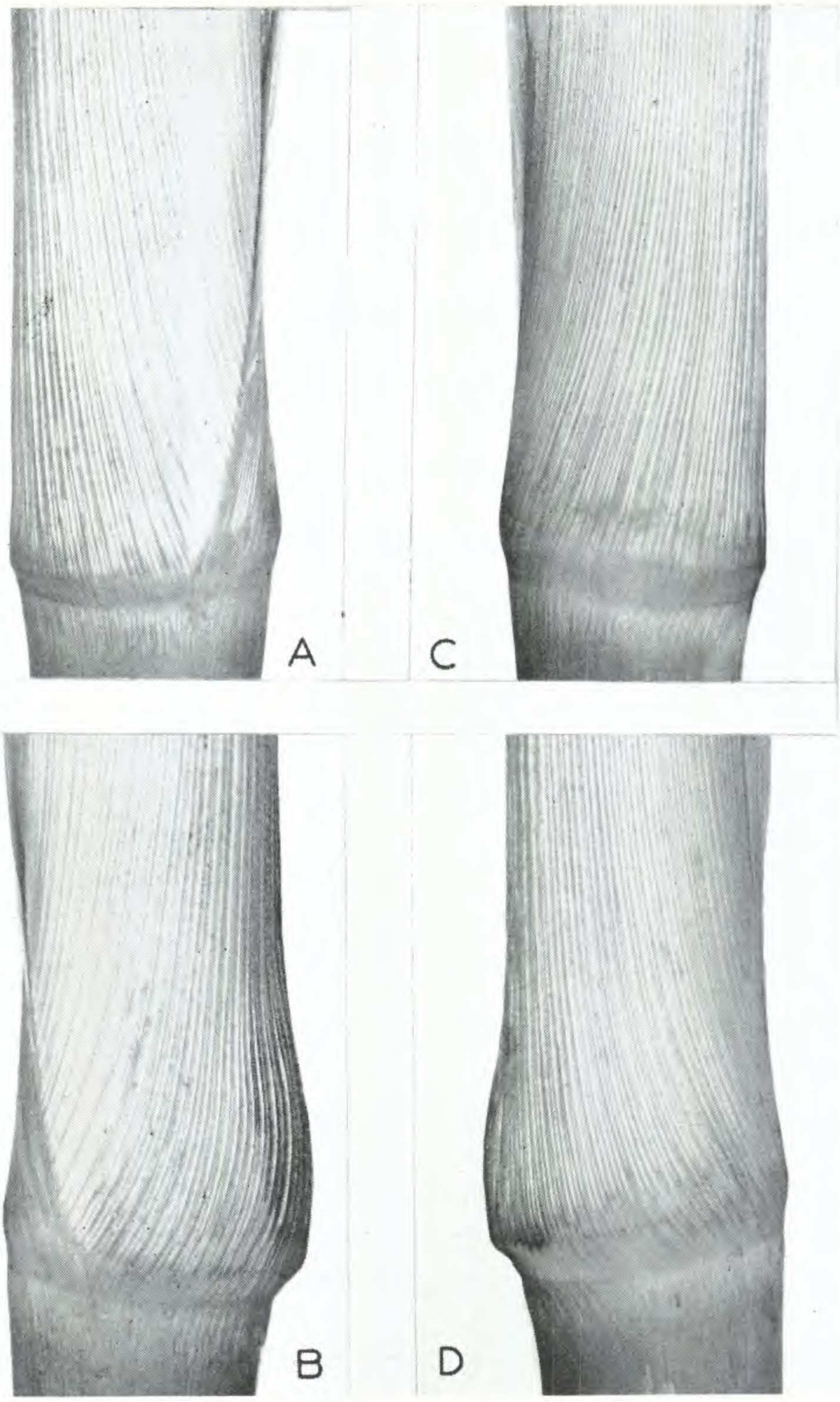

WEATHERWAX—RIGHT- AND LEFT-HANDED CORN

Fig. 2. *A* and *B*, two consecutive nodes of a corn plant, as seen from the same side of the stem. Note that in *A*, the left side of the sheath overlaps the right, and that in *B* the overlap is in the opposite direction. In *C* and *D*, the same nodes are shown from the other side of the stem.